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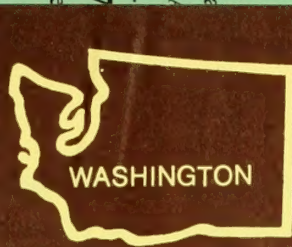
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USDA FOREST SERVICE RESEARCH NOTE

PNW-166

September 1971

INHERITANCE OF STOCKINESS IN PONDEROSA PINE FAMILIES

by

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ABSTRACT

Diameters at average seedling height of 31.25 centimeters among 41 families were 22 percent greater from stocky parents than from slender parents, though average heights were not significantly different. Low relationship between stockiness and height suggests that selection for tall stocky types is feasible. About 19 percent of the deviation of volumes of 3-year-old progeny from a common regression on height was attributable to parental type.

Keywords: Tree genetics, ponderosa pine,
tree diameter measurement.

INTRODUCTION

Inheritance of stockiness or slenderness, so commonly observed in animals and plants, has also been observed in trees, particularly ponderosa pine. The trait has received little attention from forest geneticists but deserves more.

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Weidman^{1/} observed striking slenderness differences among 20 ponderosa pine races in an Idaho study. Squillace and Silen^{2/} defined taper as average height of a race for a 6-inch diameter tree and estimated broad sense heritability of taper differences at 0.41 among 10 races of ponderosa pine studied in Oregon and Washington. Racial differences, however, are not as useful to the tree breeder as would be the inherent differences in stockiness transmitted by an individual parent to its offspring. This study explores the inheritance of a similar trait, average diameter at a given height, in 3-year-old families from selected phenotypically stocky and slender parent trees.

Height-adjusted diameter is more than just another expression of diameter. Figure 1 illustrates two seedling families grown at the same spacing where there is a difference in diameter at each height. Such genetic control

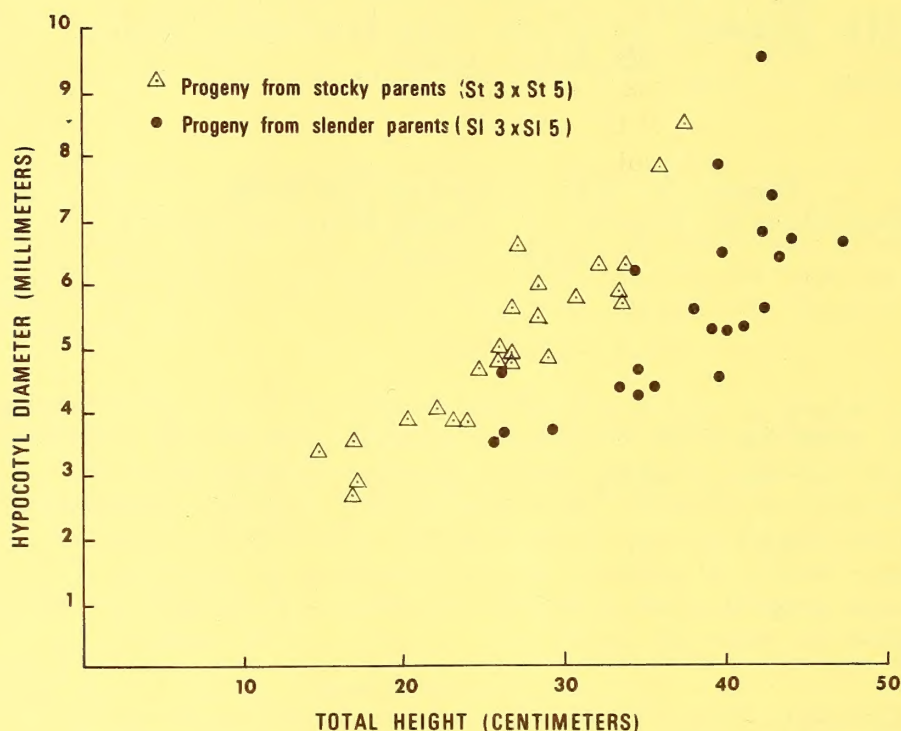


Figure 1.--Seedling height and diameter for a stocky and a slender family from the study illustrate a case in which, at each height, the stocky family consistently has diameter greater than the slender family.

^{1/} R. H. Weidman. Evidences of racial influence in a 25-year test of ponderosa pine. J. Agr. Res. 59: 855-887, illus. 1939.

^{2/} A. E. Squillace and R. R. Silen. Racial variation in ponderosa pine. Forest Sci. Monogr. 2, 27 p. 1962.

over diameter could be an important volume component of inherent growth differences, particularly if the trait is as highly heritable for families as initially estimated for races.

METHODS

In 1964, seven pairs of adjacent open-grown parents about 40 years old were selected at 3,800-foot elevation in the Kiwa Springs area near Bend, Oregon, for striking phenotypic difference in stem form^{3/}. The more stocky parent-tree of each pair was larger in diameter and had distinctly more volume than the more slender parent-tree, even though it was generally shorter or of nearly equal height (table 1). Past height and diameter of each parent at 5-year intervals was estimated from stem analyses.

In April, pollen-proof bags were placed over female strobili on 10 trees that were flowering in 1964 (pairs 3, 4, 5, and 6, plus stocky parent 1 and slender parent 7). There was sparse flowering in some parents, and it was possible to make only part of the possible crosses and mixed pollen matings as listed in table 2. Seed, collected in October 1966, included nine wind-pollinated lots.

Seedlings were grown 3 years in coldframes at 2- by 2-inch spacing. Total heights and caliper at a point 1 cm. below the cotyledons were made yearly, but only data for age 3 years are reported here. Twenty-seven seedlings were measured in most families, and families with fewer than 15 survivors were not analyzed.

Objectives of the analysis were to ascertain if there were inherent differences in diameters of a family for seedlings of average height (31.25 cm.), if stocky parents produced inherently stockier offspring, if any such differences were closely related to family height, and if a useful component of family volume differences was related to inherent stockiness.

Relationship between seedling height and diameter was nonlinear and variability in diameter increased with height (see fig. 1, for example). An extensive investigation of possible transformations suggested that the linear

^{3/} Dr. Carl Berntsen, then project leader, and Walter Dahms, now project leader, of the Silvicultural Laboratory, Bend, Oregon, selected and made stem analysis of parent trees, assisted with pollinations, and otherwise expedited the study.

Table 1.--Tree measurements of stocky-slender ponderosa pine parents,
December 1966

Pair number	Tree	Volume ^{1/}	D.b.h., d.i.b.	Total height
		<i>Cubic feet</i>	<i>Inches</i>	<i>Feet</i>
1	Stocky 1	14.4	12.0	37.8
	Slender 1	10.9	9.3	44.1
2	Stocky 2	29.3	14.5	50.6
	Slender 2	18.6	12.4	50.5
3	Stocky 3	27.6	17.1	36.9
	Slender 3	20.6	13.2	48.8
4	Stocky 4	37.3	18.3	54.9
	Slender 4	18.8	12.8	48.2
5	Stocky 5	34.5	16.8	52.6
	Slender 5	26.7	14.1	55.0
6	Stocky 6	14.6	12.4	36.9
	Slender 6	8.9	9.3	36.6
7	Stocky 7	31.5	14.5	55.1
	Slender 7	23.1	12.8	56.1
Average	Stocky	27.03	15.09	46.40
Average	Slender	18.23	11.99	48.47

^{1/} Total wood volume inside bark from ground to terminal bud estimated from stem analysis.

regression of inverse diameter on height was the best method of adjusting the diameters of different families to an expected diameter at a common height. Stockiness (or slenderness) was then analyzed as predicted inverse diameter at a height of 31.25 cm. Family mean volume was calculated from heights and diameters of individual seedlings by considering the seedling to be conical in form.

Since only a fraction of the possible crosses were made, it was necessary to use a least squares analysis to obtain estimates of the average

Table 2.-- Height, diameter, diameter at 31.25-centimeter height, and volume of 3-year-old families studied for stockiness trait

Parents	Stocky x stocky				Slender x slender				Combined			
	Height		Diameter		Height		Diameter		Height		Diameter	
	Om.	Mm.	@ 31.25 cm.	Mm.	Om.	Mm.	@ 31.25 cm.	Mm.	Om.	Mm.	@ 31.25 cm.	Mm.
			Volume	Cu. cm.			Volume	Cu. cm.			Volume	Cu. cm.
1x4	37	7.6	6.1	6.3	--	--	--	--	--	--	--	--
1x5	26	5.5	5.8	3.1	--	--	--	--	--	--	--	--
3x4	34	5.9	5.0	3.7	33	5.4	4.6	2.9	--	--	--	--
3x5	25	4.7	5.8	1.7	37	5.7	4.5	3.5	--	--	--	--
3x7	--	--	--	--	33	4.9	4.1	2.8	--	--	--	--
4x3	31	5.4	5.1	2.7	--	--	--	--	--	--	--	--
4x5	35	5.9	4.6	3.7	--	--	--	--	--	--	--	--
4x6	33	5.4	5.1	2.8	--	--	--	--	--	--	--	--
5x4	--	--	--	--	36	5.5	4.2	3.6	--	--	--	--
5x6	--	--	--	--	34	5.4	4.7	3.0	--	--	--	--
5x7	--	--	--	--	37	5.2	3.9	3.1	--	--	--	--
6x4	--	--	--	--	36	5.8	4.5	3.6	--	--	--	--
6x5	--	--	--	--	32	4.7	4.1	2.2	--	--	--	--
6x7	--	--	--	--	32	5.4	5.1	2.7	--	--	--	--
7x6	--	--	--	--	32	5.5	5.1	2.9	--	--	--	--
1xm1/	30	6.0	5.4	3.6	--	--	--	--	--	--	--	--
3xm	24	4.1	4.8	1.2	--	--	--	--	--	--	--	--
3xm2/	--	--	--	--	34	5.4	4.4	3.5	--	--	--	--
4xm	35	5.7	4.2	4.1	--	--	--	--	--	--	--	--
5xm	38	6.5	5.1	4.7	30	5.0	4.8	2.2	--	--	--	--
6xm	33	5.6	4.8	3.0	27	4.9	5.2	2.1	--	--	--	--
7xm	--	--	--	--	29	4.8	4.9	2.0	--	--	--	--
1xop3/	33	5.9	5.1	3.4	--	--	--	--	--	--	--	--
3xop	35	5.5	4.8	3.3	33	4.6	4.1	2.2	--	--	--	--
4xop	36	5.4	4.2	3.6	--	--	--	--	--	--	--	--
5xop	35	5.8	5.2	3.4	36	4.9	4.2	2.5	--	--	--	--
6xop	27	4.7	5.1	1.8	30	4.9	4.7	2.2	--	--	--	--
7xop	--	--	--	--	31	5.3	5.0	2.8	--	--	--	--
sl3xst34/	--	--	--	--	--	--	--	--	27	4.6	5.2	1.8
sl5xst5	--	--	--	--	--	--	--	--	36	5.0	3.9	2.7
sl7xst4	--	--	--	--	--	--	--	--	38	5.9	4.3	4.0
st6xsl4	--	--	--	--	--	--	--	--	39	6.8	4.7	5.5
st6xsl6	--	--	--	--	--	--	--	--	30	5.0	4.8	2.3
st6xslm	--	--	--	--	--	--	--	--	32	5.0	4.6	2.4

- 1/ A pollen mix of stocky parents 3, 4, 5, and 6 used on all crosses with stocky female parents.
2/ A pollen mix of slender parents 1, 5, 6 and 7 used on all crosses with slender female parents.
3/ Open-pollinated.
4/ Slender parent is designated Sl and stocky parent St in mixed parentage matings.

diameter, stockiness, height, and volume of families of each parent. It was not possible to estimate or adjust for the effects of the specific combinations of parents. A listing of family means for the crosses involving each parent and contrasts between four completed pairs are presented in table 3.

Table 3.--Least-squares estimates of family means of crosses involving stocky or slender parents, mixed pollen matings, open pollinations, and pair differences. Differences are shown for the four complete pairs.

Parents ^{1/}	Hypocotyl diameter	Adjusted diameter at 31.25 cm. height		Height	Volume
		Inverse	Actual		
	Mm.	-----Mm.-----		Cm.	Cu. cm.
St1	6.16	0.1735	5.76	30.5	3.90
St3	4.93	.1878	5.32	27.7	2.16
St4	5.99	.2184	4.58	36.1	4.06
St5	5.55	.2037	4.91	32.7	3.16
St6	5.37	.2016	4.96	31.6	2.82
Sl3	5.16	.2284	4.38	33.2	2.87
Sl4	6.06	.2168	4.61	36.0	4.16
Sl5	5.30	.2283	4.38	34.4	3.01
Sl6	5.27	.2040	4.90	30.9	2.65
Sl7	5.41	.2122	4.71	32.7	3.05
StMix	5.45	.2193	4.56	33.0	3.22
SlMix	5.18	.2038	4.91	30.5	2.69
Open	5.22	.2167	4.61	33.0	2.83

Pair differences (stocky minus slender)

3	-.24	-.0406***	+.94	-5.50*	-.71
4	-.07	+.0015	-.03	+.07	-.11
5	+.25	-.0245*	+.53	-1.78	+.15
6	+.10	-.0025	+.06	+.74	+.17
Average	+.01	-.0165***	+.39	-1.62	-.12

^{1/}

Slender parent is designated Sl and stocky parent St.

* P < 0.05.

*** P < 0.001.

Linear regressions of log-volume on height were calculated and are presented in table 4. Comparisons of separate regressions for each of the five family types indicated that there was no significant difference between them and a common regression coefficient was therefore appropriate. Comparisons of volume are the comparisons between the intercepts of the prediction equation.

Table 4.-- \log_e volume regressed on height with a common regression coefficient and predicted volume at 31.25-centimeter height

Family type	Number of families	Prediction equation for \log_e volume ^{1/}	Predicted volume at 31.25-cm. height
Stocky crosses	12	$-1.304 + 0.077 H$	3.01
Slender crosses	14	$-1.507 + .077 H$	2.46
Stocky x slender crosses	6	$-1.522 + .077 H$	2.42
Open-pollinated stocky	5	$-1.454 + .077 H$	2.59
Open-pollinated slender	4	$-1.616 + .077 H$	2.20

^{1/} H = height in centimeters.

RESULTS

Other than inheritance, there was no reason to expect significant variation in the average family diameters of seedlings of average height (31.25 cm.). Hence, to find in a population of only 10 parent trees such extreme differences as those between height-adjusted diameter of all families from stocky parent 1 (5.76 mm.) and those from slender parent 3 (4.38 mm.) in table 3 is strong evidence that the trait shows appreciable heritable variation from parent to parent in a natural population.

At age 3, families resulting from crosses of stocky parents averaged about 11 percent larger diameter at 31.25-cm. height than families of crossed slender parents. Among the four parental pairs which bore cones, the stocky parent produced significantly stockier offspring in two cases ($P < 0.001$ and $P < 0.05$) and equally stocky progeny in the other two cases. Even actual average diameter of the families reflected the stockiness of the parental type. Overall, the 17 families of various stocky parentage were larger in actual diameters than the 18 families from slender parentage (5.62 mm. vs. 5.18 mm.). Conversely, they were somewhat shorter in height (32.18 cm. vs. 32.88 cm.). The common association of slenderness with tallness and stockiness with shortness, as seen in humans, is thus also displayed in these families. As shown in figure 2, there is a negative relationship of mean family height to mean family diameter adjusted to a common height of 31.25 cm. ($r = -0.47$).

As expected, mean family height and unadjusted diameter was positively related ($r = 0.66$). Although contrast in slope of the two regressions is interesting, the important point is that large height-adjusted diameters commonly occur among tall families. Among the tallest families, for example

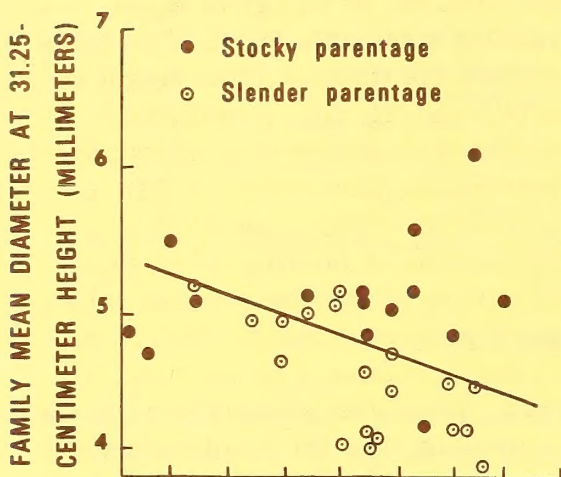
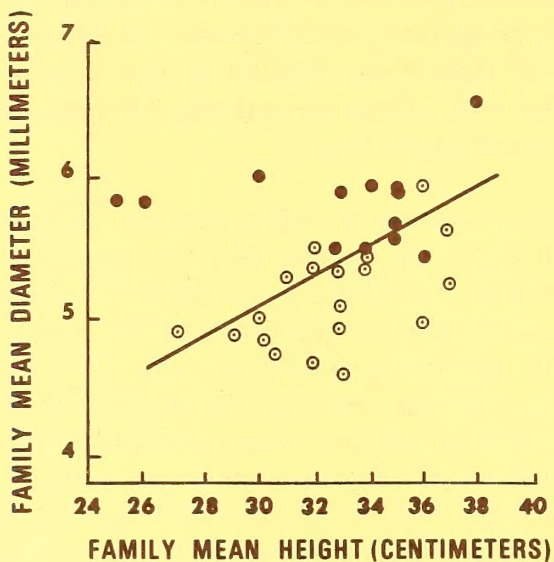


Figure 2.--Relationship of height and diameter at 31.25-cm. height showing slender-tall and stocky-short tendencies of the 41 family means. Average family diameters increase with height as expected.



those over 36 cm. in average height, there occur not only very slender (4.0-mm. diameter) but also very stocky (6.15-mm. diameter) families, suggesting that breeding simultaneously for tallness and stockiness is practical.

Volume of stocky families, when compared for seedlings of equal height, was greater. The common regression applicable for the five types of families allowed the comparison of average log volume of any height as the difference between the intercepts (table 3 and fig. 3). Families of stocky parents had significantly more volume than did families of slender parents ($P < 0.01$), open-pollinated slender female parents ($P < 0.01$), or crosses of stocky with slender parents ($P < 0.05$). When compared at a height of 31.25 cm., the expected average volume of families of stocky parents was 22 percent greater than for families of slender parents, whereas unadjusted average volumes averaged only 2 percent greater. Two other comparisons seem worthy of mention to show consistency of the trait, although they are not statistically significant. When both parents were stocky, volume was 16 percent greater for their offspring than for families of open-pollinated stocky parents, and families of open-pollinated stocky parents had 18 percent more volume than families of open-pollinated slender parents. About 19 percent of the total deviation of volumes from the common slope of regression on height was attributable to the five parental types shown in table 4.

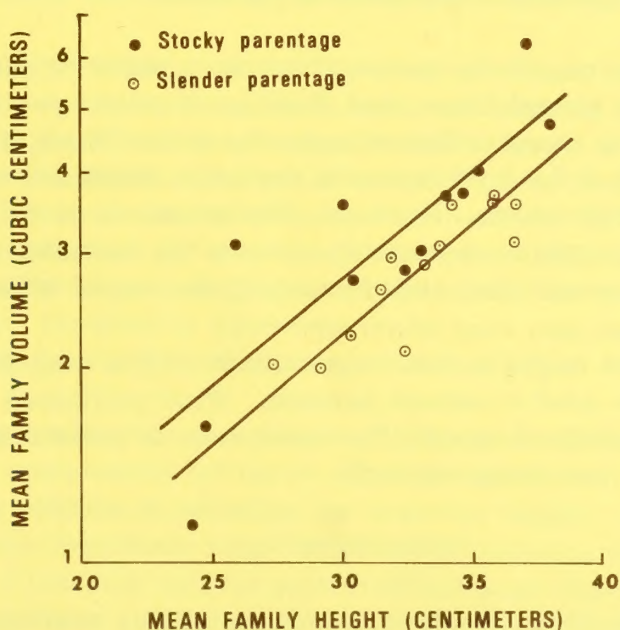


Figure 3.--Mean family volume versus height of crosses among stocky and slender parents.

These observations suggest appreciable correlation between 40-year-old parents and 3-year-old offspring. Attempts to directly relate 1966 parental diameter to the height-adjusted measure of offspring stockiness were singularly unsuccessful ($r = -0.09$). However, since yearly parental heights and diameters were estimated from stem analyses, a number of other measurements were tried as linear predictors of family stockiness. Surprisingly, no parental function of diameters or volumes was highly correlated to family stockiness. For example, relationship of estimated parental diameter as a common height of 40 feet with corresponding height-adjusted family diameters approached but did not quite attain significance ($r = 0.54$ with 8 degrees of freedom). However, functions of heights alone at various ages were highly related, i. e., good height growth of the parent was related to family slenderness. The most effective use of a height function regressed on family stockiness appears to be in the form of growth rate as linear and quadratic regression coefficients for height regressed on age. Regression on the linear coefficients accounts for 80 percent of the variation in offspring family stockiness. The addition of the quadric coefficients--a measure of the acceleration or deceleration in height growth--accounts for a surprising 91 percent of the variation. Nonetheless, these parent-offspring relationships, based on so few parent trees, should be considered primarily for their suggestion value in future research.

Selection of parent trees, even with the restriction of having to find adjacent pairs of trees of similar height, appears to have been fairly effective in identifying genetic differences in the trait.

For the seven pairs, stocky parent trees were about 30 percent stockier than slender parent trees, and families of stocky parents appeared to be about 22 percent stockier than slender families. Thus, it appears that about two-thirds of the differences in the adult stockiness trait was inherited as juvenile differences. However, the intraclass correlation is 0.46. The latter estimate is reasonably close to the heritability of 0.41 estimated by Squillace and Silen (see footnote 2) for racial differences.

Future selections might be even more effective if a wind-pollinated nursery test could be used to screen parents. Wind-pollinated families in the study reflect inherent taper differences seen in outcrossed families ($r^2 = 0.72$ based on nine comparisons).

DISCUSSION

With inheritance of the stockiness trait tentatively verified from individual ponderosa pine parents as well as races, and the trait seemingly

so potentially responsive to simple selection, several new questions become important.

Are stocky families necessarily shorter? Although the highly significant regression in figure 2 would suggest so, only 43 percent of the relationship is explained by the regression. Squillace and Silen (see footnote 2) also found height and taper to be of low correlation in racial data. Of importance to the forester, however, are the plentiful exceptions. Of the 17 outcrossed families, for example, the two tallest were from stocky parentage and among the highest in volume and stockiness. The indication here is that there need be no penalty in selecting the tall stocky type except, perhaps, that stockiness may be associated with limbiness. Of course, it remains to be seen whether this combination of traits will remain true for adult volume, or whether the tall stocky type is desirable in terms of adult volume per acre.

Will stockiness or slenderness persist in these families to maturity? Selection in 40-year-old parents was effective in reproducing the same trait in the seedling family, an indicator of appreciable juvenile-mature correlation. Squillace and Silen (see footnote 2) provide data from 1939-56 observations on ponderosa pine races to show a high correlation ($r = 0.77$, computed from data in their table 10, page 20) of the trait measured over a 17-year interval. Presumably the trait is fairly stable. Long-term observation of the families of our study now planted in spacing tests near Bend will ultimately provide juvenile-mature correlations.

If we speculate further, a most important and basic question concerns relationships between inherent growth rates and inherent differences in stockiness. Can the effective selection for differences in stockiness as demonstrated in this study provide a shortcut for selection for better volume growth? Tree volume is more influenced by diameter than by height. As figure 3 shows, selection for stockiness alone provided increased volumes, accounting for about 19 percent of the family volume deviation from the common regression. No similar increases would have resulted from parental selections based upon height, diameter, or volume.

It seems inevitable that a metric trait like tree volume growth will be partitioned into components for more effective selection. Thus, this study suggests that in addition to selection for superior height, a further selection for the stockiness component might improve efficiencies for volume breeding. Perhaps some of inherent volume growth differences observed in other studies reflect this component. These conjectures depend ultimately on the outcome of the question, "Assuming equal heights, can equal numbers of stocky or

slender trees grow on an acre?" Even though the 3-year-old seedlings displayed family differences in stockiness at equal spacing, only long-term observation of stocky and slender families at various spacings will provide a final answer. Meanwhile, the trait deserves more exploration by the tree breeder.